# Suture Index and Growth in the Male South African Fur Seal, *Arctocephalus pusillus* (Pinnipedia: Otariidae)

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The South African furs seal (*Arctocephalus pusillus pusillus*) is very closely related to the Australian fur seal (*A. pusillus doriferus*). We examine the relationship between skull suture index (**SI***) and growth parameters in the male South African fur seal, based on 42 animals of known age ranging from 10 m to 11 y 11 m. Twenty one (21) animals were aged based upon tagging as pups and 21 were aged based on dentine growth layers (1 to 11 y). Suture index and morphometric information was available on an additional 27 males; 17 had no age information but 10 were known from their dentition to be ≥12 y. Age has previously been found to be approximately directly proportional to suture index. Here we estimate asymptotic size and growth kinetics from **SI*** using nonlinear growth models [exponential saturation (von Bertalanffy), Logistic, Gompertz] fitted to cross-sectional morphometric data (n = 8 variables). The relationship between the following measurements was examined and suture index are presented in the present study: external body (standard body length, **SBL**; length of front flipper; length of hind flipper), skull (condylobasal length, **CBL**; Bizygomatic breadth; mastoid breadth; length of Mandible or Ramus length) and baculum (bacular length, **BL**). The asymptote values of these parameters are compared to those derived from chronological age and show very good agreement. The growth kinetic parameters calculated in terms of **SI*** when converted into years using the relationship between **SI*** and true Age (y) are also in close agreement with those calculated on tag and dentition aged animals.

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KEYWORDS: age-determination, asymptotic size, body measurements, maturity classification, Otariidae, Pinnipeds, skull suture, suture index.

## INTRODUCTION

Skull suture characteristics have been shown to give a good indication of age class or maturity of male South African fur seals (*Arctocephalus pusillus pusillus*) and suture index (**SI***) can give approximate estimates of the age of the animals (Stewardson et al. 2011). Sutures in South African fur seals do not close in a definitive order (Stewardson et al. 2011) and so using order of suture closure to determine relative ages of male seals is only approximate (cf. Rand 1949, 1956; Brunner, 1998a,b; Brunner et al. 2004). The major limitation of the method, however, is that the relationship between suture scores of individual sutures and suture index (**SI***) and age is not known for very old animals (≥12 y). Suture information is available on animals that must be considerably older than the oldest animal of definitively known age. It is therefore useful to investigate the relationship between suture index (**SI***) and growth parameters such as Condylobasal length (**CBL**) of the skull, standard body length (**SBL**) and skeletal measurements.

Examination of growth and development of the skeleton was thought to be one of the more useful methods of estimating relative age in older specimens of fur seals (Rand 1949, 1956; Jonsgard 1969; McCann 1993; McLaren 1993) but statistical studies (Stewardson 2001; Stewardson et al. 2008, 2009, 2010a, b) have shown that skull and skeletal measurements give an indication of "age class" rather than chronological age. Skull, skeletal measurements, Standard Body length (**SBL**) and even baculum measurements can all be successfully used to classify South African fur seals into pups, juveniles, subadults and adults if the sex is known (Stewardson et al. 2008, 2009, 2010a,b). If the sex is not definitely known difficulties would arise in distinguishing a subadult male from a female (Stewardson 2001; Stewardson et al. 2010a).

The specific objective of this study was to estimate asymptotic size inferred from suture index using nonlinear growth models fitted to cross-sectional morphometric data. There is no comparable information on development of body size parameters vs. suture closure parameters in the Australian fur seal (*Arctocephalus pusillus doriferus*), which is very closely related to the South African fur seal (*Arctocephalus pusillus pusillus*) (Lento et al. 1997; Brunner 1998a,b; Brunner et al. 2002; Brunner 2004; Brunner et al. 2004; Stewardson et al. 2008, 2009, 2010a,b, 2011) and so any information gained on the South African fur seal would be useful for studies of the life history of the Australian fur seal (Arnould and Warneke 2002). Adult male Australian fur seals are known to reach a marginally larger size than the South African variety and grow faster and perhaps live longer (Arnould and Warneke 2002; Stewardson et al. 2008, 2009) and so some caution is needed using data on South African fur seals to draw inferences about Australian fur seals.

## MATERIALS AND METHODS

### Abbreviations used in Text

Full Suture Closure (**FSC**), Partial Suture Closure (**PSC**), Condylobasal length (**CBL**), Standard Body length (**SBL**), Suture Index (**SI**), Coefficient of Determination (**$R^2$**).

### Collection of specimens and morphometry

Male South African fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S, 27° 54'E), from August 1978 to December 1995, and accessioned at the Port Elizabeth Museum (PEM). Collection procedures are described in Stewardson et al. (2008, 2009). Forty eight (48) males had suture index (**SI**) information; external body information was available on 43 males (body measurement information missing on PEM 898, 1453, 1698, 2047 & 2258); skull data was available on 44 animals (but suture information was missing on PEM2035, 2141, 2151 & 2252). Matched baculum data and suture index information was available on only 35 animals (13 male specimens with suture data, had no baculum information).

Thirty one (31) specimens were aged from incremental lines (called Growth Layer Groups, **GLG**) observed in the dentine of upper canines (Oosthuizen 1997; Stewardson et al. 1998; Arnould and Warneke 2002; Stewardson et al. 2008, 2009, 2011). Ten (10) of the 31 GLG-dentine-aged animals could only be classified as being ≥12 y old (Stewardson et al. 2011). Occasional individuals are found where 13 GLGs can be distinguished (PEM2151) and so their minimum age is ≥13 y but such animals are rare. Attempts to age the remaining seventeen (17) animals from tooth sectioning were not successful.

The sample was supplemented with external body and skull measurements from 21 known-age animals (animals tagged as pups) from Marine and Coastal Management (MCM), Cape Town. Most specimens in the MCM collection had very complete data sets with the exception of MCM1809, which had only information on tag-age, suture indices for the skull sutures, condylobasal length (**CBL**) and standard body length (**SBL**). No baculum data was available on any of the MCM specimens.

The total number of animals with suture information was 48 + 21 = 69 animals but many animals had incomplete sets of information on other skull and body measurements. For example, the difference in the data set for sutures and **CBL** (n = 65) and sutures and **SBL** (n = 64) is not simply due to a single missing **SBL** measurement. All MCM animals had information on sutures and **CBL** and **SBL.** In the PEM data set in one animal both **CBL** and **SBL** data were missing, in 4 animals **CBL** data was available and **SBL** data was not and in 3 other animals **SBL** data was available and **CBL** was not. Thus, in the case of skull measurements, 65 animals had information on sutures and **CBL** but 4 lacked **CBL** information because of skull damage.

The relationship between the following measurements was examined and suture index are presented in the present study: external body (standard body length, **SBL**; length of front flipper; length of hind flipper), skull (condylobasal length, **CBL**; Bizygomatic breadth; mastoid breadth; length of Mandible or Ramus length) and baculum (bacular length, **BL**). Measurements were recorded according to Stewardson et al. (2008, 2009, 2010a,b). Statistics on Tip of Snout to Genital Opening and Tip of Snout to Anterior Insertion of Front Flipper vs. suture index were investigated by Stewardson (2001) but provided little novel extra information and so have been omitted from the present study.

To make curve fitting easier in the present study, the suture scores were recoded as ranging from 0-3 (fully open, 0; suture less than half closed, 1; suture more than half-closed, 2; fully closed, 3). These values were added to give a total suture index (**SI***), ranging from 0 (all sutures open) to 33 (all sutures closed). The special form of the suture index used in the present study is designated **SI***. The highest **SI*** on a male of definitive age was **SI*** = 16 for an individual 11 y 11 months old (MCM1809). The highest **SI*** readings were **SI*** = 22 for an animal ≥ 12 y based upon GLG-dentine (PEM1698) and another specimen (PEM1587) of unknown age.

### Asymptotic size

Asymptotic size, inferred from suture index (**SI***), was estimated by fitting three nonlinear growth curves [Exponential Saturation (sometimes called the von Bertalanffy equation), Logistic and Gompertz curves, Stewardson et al. 2009] to morphometric data (Tables 3 and 4 below). The data on Front and Rear Flipper vs. **SI*** were found to be described very well by simple linear regressions of the form y = mx + b. The nonlinear and linear growth curves were fitted using EXCEL routines and the SOLVER least squares fitting routine in EXCEL (Stewardson et al. 2008, 2009, 2010a,b). Asymptotic errors of the fitted parameters were calculated by matrix inversion as previously described (Stewardson et al. 2008, 2009, 2010a,b).

## RESULTS

### Suture Closure vs. Condylobasal length (CBL) and Standard Body Length (SBL)

The relationship between **SI*** and **CBL** (Table 1) was examined using animals 80-201 cm **SBL** and ages 10 months to 11y 11 months upon tagging (n = 21) and the animals with a definitive age (< 12 y) based upon GLG-dentine (n = 21). **CBL**s were classed into groups rounded off to the nearest 10 mm (range 160 mm to 240 mm). For the range of available specimens, the sequence of partial suture closure (**PSC**) according to **CBL** was Basioccipito-basisphenoid (VI), Occipito-parietal and Coronal (I & V), Squamosal-jugal (X), Interparietal (III), Premaxillary-maxillary (IX).

Table 2 shows the data on **SI*** vs. **SBL** classed into groups rounded to the nearest 10 cm (range 84.5 to 199 cm). Two males from the Port Elizabeth museum collection (PEM2036 & PEM 2252) had no **SBL** measurements and so the data set consists of 21 animals with ages based on tagging but only 19 animals with GLG-dentine-based ages. For the range of available specimens, the sequence of **PSC** according to **SBL** was Basioccipito-basisphenoid (VI), Occipito-parietal/Coronal (I & V), Squamosal-jugal (X), Interparietal (III) and Premaxillary-maxillary (IX) in the oldest tag-aged animal. The other sutures were partially (**PSC**) or completely closed (Full suture closure, **FSC**) only in animals ≥12 y-old. The order of closure appeared to be Squamosal-parietal/ Interfrontal (II & IV) and then the Maxillary (VII). The Basisphenoid-presphenoid (VIII) and Internasal (XI) showed no signs of closure in the specimens used in the present study but have been reported to close in very old South African fur seal males (Rand 1949).

The sequence of **FSC** (suture score = 3 in the present study) for animals placed in groups according to **SBL** was Basioccipito-basisphenoid (VI), Occipito-parietal (I), Interparietal (III), Coronal (V), Squamosal-jugal (X) and finally the Premaxillary-maxillary (IX). The Basioccipito-basisphenoid (VI) was fully closed in all animals ≥ 150 cm **SBL** and nearly all animals with a **CBL** > 200 mm. **FSC** was evident in some animals in the 120 cm **SBL** and 190 mm **CBL** classes. The Occipito-parietal (I) was fully closed in all animals with an **SBL** greater than 170 cm, with **FSC** evident in some animals in the 130 cm **SBL** class. The Interparietal (III), Coronal (V) and Squamosal-jugal (X) were closed in some animals in the 170 cm **SBL** size class. The Maxillary (VII), Premaxillary-maxillary (IX), Squamosal-parietal (II), Interfrontal (IV), Basisphenoid-presphenoid (VIII) and Internasal (XI) showed no signs of closure in any animals less than 12 y-old. The male PEM2049 (**CBL** 262.7 mm, **SBL** 174 cm) was the smallest animal with any closure of these sutures.

### Relationship between Skull and Body Parameters and Suture Index

Estimated asymptotic **SBL** was calculated using animals 80-201 cm, using all the animals with **SI*** information (n = 64). Parameters for the three growth functions are given in Table 3. Inspection of the residuals versus fitted values plots indicated that the three models (Exponential, Logistic and Gompertz) were all adequate for the range of **SI*** values available. In terms of the coefficient of determination ($R^2$), the models were found to be quite similar and the plotted curves largely overlap so they cannot be distinguished. Most $R^2$-values are ≈ 0.8 or higher and so fit the data very well. All three of these models adequately described the 'general' growth pattern of the Condylobasal length (**CBL**), Ramus length, Bizygomatic breadth, Mastoid breadth, Standard Body length (**SBL**) and baculum length (**BL**) vs. Suture Index (Table 3). Fig. 1 is a plot of Condylobasal length (**CBL**) vs. **SI*** and Fig. 2 is a plot of Standard Body Length (**SBL**) vs. SI.

**Table 1: Suture Scores and Suture Index (SI*) for classes of Condylobasal Length (CBL) for male South African Fur Seals. Suture data for animals with known chronological age (y) based on tagging (Marine and Coastal Management (MCM) collection, Cape Town) and dentition (Port Elizabeth Museum, PEM). Suture number system (I-XI) and suture scores procedure as for Stewardson et al. (2011). Each CBL size class is rounded to the nearest 10 mm.**

| | Condylobasal Length Class (mm) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Suture & Suture Nº | 160 | 170 | 180 | 190 | 200 | 210 | 220 | 230 | 240 | 250 | 270 |
| Basioccipito-basisphenoid (VI) | 0,0 | 0 | 1,3 | 3,1 | 3,3,2,2 | 3,3,3,3 | 3,3,2,3,3,3 | 3,2,3,3,3,3,3,3,3 | 3,3,3,3,3,3,3,3 | 3,3,3 | 3 |
| Occipito-parietal (I) | 0,0 | 0 | 0,2 | 2,1 | 2,1,2,1 | 3,2,3,3 | 3,3,3,3,3,3 | 2,2,2,3,3,2,3,2,3 | 3,3,3,2,3,3,2,3 | 2,2,3 | 3 |
| Coronal (V) | 0,0 | 0 | 0,2 | 1,0 | 1,1,1,1 | 1,2,0,2 | 1,1,2,1,1,2 | 1,2,0,1,1,1,1,2,2 | 3,3,2,2,2,2,1,0 | 3,3,2 | 2 |
| Interparietal (III) | 0,0 | 0 | 0,1 | 0,0 | 0,1,1,1 | 1,1,0,1 | 0,1,2,1,1,2 | 1,1,1,0,1,1,0,0,2 | 3,3,2,1,2,1,1,1 | 1,3,2 | 1 |
| Squamosal-jugal (X) | 0,0 | 0 | 0,0 | 0,0 | 0,0,0,0 | 0,0,0,0 | 0,0,0,0,0,0 | 0,0,0,1,1,0,0,1,0 | 0,3,1,0,0,0,0,0 | 0,1,1 | 1 |
| Premaxillary-maxillary (IX) | 0,0 | 0 | 0,0 | 0,0 | 0,0,0,0 | 0,0,0,0 | 0,0,0,0,0,0 | 0,0,0,0,0,0,0,0,0 | 0,1,0,0,0,0,0,0 | 0,0,0 | 0 |
| Maxillary (VII) | 0,0 | 0 | 0,0 | 0,0 | 0,0,0,0 | 0,0,0,0 | 0,0,0,0,0,0 | 0,0,0,0,0,0,0,0,0 | 0,0,0,0,0,0,0,0 | 0,0,0 | 0 |
| Squamosal-parietal (II) | 0,0 | 0 | 0,0 | 0,0 | 0,0,0,0 | 0,0,0,0 | 0,0,0,0,0,0 | 0,0,0,0,0,0,0,0,0 | 0,0,0,0,0,0,0,0 | 0,0,0 | 0 |
| Interfrontal (IV) | 0,0 | 0 | 0,0 | 0,0 | 0,0,0,0 | 0,0,0,0 | 0,0,0,0,0,0 | 0,0,0,0,0,0,0,0,0 | 0,0,0,0,0,0,0,0 | 0,0,0 | 0 |
| Basisphenoid-presphenoid (VIII) | 0,0 | 0 | 0,0 | 0,0 | 0,0,0,0 | 0,0,0,0 | 0,0,0,0,0,0 | 0,0,0,0,0,0,0,0,0 | 0,0,0,0,0,0,0,0 | 0,0,0 | 0 |
| Internasal (XI) | 0,0 | 0 | 0,0 | 0,0 | 0,0,0,0 | 0,0,0,0 | 0,0,0,0,0,0 | 0,0,0,0,0,0,0,0,0 | 0,0,0,0,0,0,0,0 | 0,0,0 | 0 |
| **Suture Index (SI*)** | **0,0** | **0** | **1,7** | **6,2** | **6,6,6,5** | **8,8,6,9** | **7,8,7,8,8,10** | **7,7,6,8,9,7,7,8,10** | **12,16,11,8,10,9,7,7** | **9,12,11** | **9** |
| **Age Class (y)** | **1,1** | **2** | **2,8** | **3,4** | **3,4,4,4** | **5,6,4,8** | **6,4,6,6,7,8** | **7,4,5,6,7,7,7,8,7** | **9,12,8,7,7,9,7,6** | **8,9,10** | **11** |
| **Total Nº Skulls = 42** | **2** | **1** | **2** | **2** | **4** | **4** | **6** | **9** | **8** | **3** | **1** |

**Table 2: Suture Scores and Suture Index (SI*) for classes of Standard Body Length (SBL) for male South African Fur Seals. Suture data for animals with known chronological age (y) based on tagging (Marine and Coastal Management (MCM) collection, Cape Town) and on dentition for the animals from the Port Elizabeth Museum (PEM). Suture numbers (I-XI) and suture scores procedure as for Stewardson et al. (2011). Each SBL size class rounded to the nearest 10 cm. Roman numerical classification of sutures follows Brunner (1998a,b).**

| | Standard Body Length Class (cm) | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Suture & Suture Nº | 80 | 90 | 100 | 110 | 120 | 130 | 140 | 150 | 160 | 170 | 180 | 190 | 200 |
| Basioccipito-basisphenoid (VI) | 0,0 | 0 | 1 | 2 | 3,3,2,1 | 3,3 | 3,3,3,3 | 2,2,3,3,3,3,3,3 | 3,3,3,3,3 | 3,3,3,3,3,3,3,3 | 3 | 3,3 | 3 |
| Occipito-parietal (I) | 0,0 | 0 | 0 | 1 | 2,2,2,1 | 1,3 | 3,3,3,3 | 2,1,3,2,3,2,3,3 | 2,3,2,2,3 | 3,3,2,2,2,3,3,3 | 2 | 3,3 | 3 |
| Coronal (V) | 0,0 | 0 | 0 | 1 | 1,1,1,0 | 1,1 | 1,1,0,1 | 2,2,1,2,1,0,1,1 | 1,2,1,2,2 | 3,3,1,2,3,2,2,2 | 3 | 2,2 | 2 |
| Interparietal (III) | 0,0 | 0 | 0 | 1 | 0,0,1,0 | 1,1 | 0,1,0,1 | 1,2,1,1,1,1,0,0 | 1,2,1,0,2 | 3,3,1,1,1,2,1,1 | 3 | 1,2 | 2 |
| Squamosal-jugal (X) | 0,0 | 0 | 0 | 0 | 0,0,0,0 | 0,0 | 0,0,0,1 | 0,0,0,0,0,0,1,0 | 0,0,0,1,0 | 0,3,0,0,0,0,0,0 | 1 | 1,1 | 1 |
| Premaxillary-maxillary (IX) | 0,0 | 0 | 0 | 0 | 0,0,0,0 | 0,0 | 0,0,0,0 | 0,0,0,0,0,0,0,0 | 0,0,0,0,0 | 0,1,0,0,0,0,0,0 | 0 | 0,0 | 0 |
| Maxillary (VII) | 0,0 | 0 | 0 | 0 | 0,0,0,0 | 0,0 | 0,0,0,0 | 0,0,0,0,0,0,0,0 | 0,0,0,0,0 | 0,0,0,0,0,0,0,0 | 0 | 0,0 | 0 |
| Squamosal-parietal (II) | 0,0 | 0 | 0 | 0 | 0,0,0,0 | 0,0 | 0,0,0,0 | 0,0,0,0,0,0,0,0 | 0,0,0,0,0 | 0,0,0,0,0,0,0,0 | 0 | 0,0 | 0 |
| Interfrontal (IV) | 0,0 | 0 | 0 | 0 | 0,0,0,0 | 0,0 | 0,0,0,0 | 0,0,0,0,0,0,0,0 | 0,0,0,0,0 | 0,0,0,0,0,0,0,0 | 0 | 0,0 | 0 |
| Basisphenoid-presphenoid (VIII) | 0,0 | 0 | 0 | 0 | 0,0,0,0 | 0,0 | 0,0,0,0 | 0,0,0,0,0,0,0,0 | 0,0,0,0,0 | 0,0,0,0,0,0,0,0 | 0 | 0,0 | 0 |
| Internasal (XI) | 0,0 | 0 | 0 | 0 | 0,0,0,0 | 0,0 | 0,0,0,0 | 0,0,0,0,0,0,0,0 | 0,0,0,0,0 | 0,0,0,0,0,0,0,0 | 0 | 0,0 | 0 |
| **Suture Index (SI*)** | **0** | **0** | **1** | **5** | **6,6,6,2** | **6,8** | **7,8,6,9** | **7,7,8,8,8,6,8,7** | **7,10,7,8,10** | **12,16,7,8,9,10,9,9** | **12** | **10,11** | **11** |
| **Age Class (y)** | **1,1** | **2** | **2** | **4** | **3,3,4,4** | **4,5** | **6,4,4,7** | **4,6,6,6,7,5,6,7** | **7,8,7,8,7** | **9,12,7,7,8,7,9,8** | **9** | **11,10** | **8** |
| **Total Nº Skulls = 40** | **2** | **1** | **1** | **1** | **4** | **2** | **4** | **8** | **5** | **8** | **1** | **2** | **1** |

**Table 3: Growth Parameters of Male South African Fur Seals Fitted to Suture Index (SI*)**

| Parameter | Fitting Model | Number of Animals (n) | Pup Size (P) | Exponential Constant (k) | Asymptotic Maximum ($E_\infty$) | Coefficient of Determination ($R^2$) | Asymptote Max.- Older than 7 y or ≥ 200 cm **SBL** |
|---|---|---|---|---|---|---|---|
| **Skull** | | | | | | | |
| Condylobasal Length (**CBL**), mm Figure 1 | Exponential | 65 | 156 ± 4.705 | -0.1115 ± 0.007527 | 276 ± 8.332 | 0.8400 | 254 ± 2.6<br>(n = 14)<br>Max. = 265.3 |
| | Logistic | | 157 ± 4.242 | -0.1719 ± 0.01893 | 268 ± 5.563 | 0.8453 | |
| | Gompertz | | 157 ± 4.570 | -0.1413 ± 0.01800 | 271 ± 6.620 | 0.8429 | |
| Ramus Length, mm | Exponential | 60 | 99.2 ± 3.861 | -0.09730 ± 0.008689 | 202 ± 8.687 | 0.8387 | 192 ± 2.9<br>(n = 13)<br>Max. = 194 |
| | Logistic | | 101 ± 3.425 | -0.1675 ± 0.01919 | 192 ± 5.162 | 0.8433 | |
| | Gompertz | | 100 ± 3.698 | -0.1320 ± 0.01797 | 196 ± 6.407 | 0.8413 | |
| Bizygomatic Breadth (Zyg), mm | Exponential | 61 | 85.23 ± 3.368 | -0.06495 ± 0.009577 | 182 ± 15.54 | 0.8057 | 149 ± 2.0<br>(n = 14)<br>Max. = 159 |
| | Logistic | | 85.87 ± 3.046 | -0.1288 ± 0.01995 | 166 ± 7.368 | 0.8098 | |
| | Gompertz | | 85.5 ± 4.274 | -0.09658 ± 0.01884 | 171 ± 9.975 | 0.8078 | |
| Mastoid Breadth, mm | Exponential | 59 | 74.1 ± 2.940 | -0.07436 ± 0.008803 | 167 ± 10.98 | 0.8436 | 138 ± 6.0<br>(n = 14)<br>Max. = 150 |
| | Logistic | | 85.87 ± 4.358 | -0.1288 ± 0.02903 | 166 ± 10.98 | 0.8470 | |
| | Gompertz | | 74.57 ± 3.159 | -0.1103 ± 0.01660 | 158 ± 7.153 | 0.8464 | |
| **Body** | | | | | | | |
| Standard Body Length (**SBL**), cm Figure 2 | Exponential | 64 | 77.1 ± 6.868 | -0.1114 ± 0.01387 | 211 ± 11.73 | 0.7688 | 199 ± 3.6<br>(n = 17)<br>Max. = 201 |
| | Logistic | | 79.2 ± 5.665 | -0.2182 ± 0.02717 | 198 ± 6.485 | 0.7815 | |
| | Gompertz | | 78.0 ± 5.753 | -0.1635 ± 0.02407 | 203 ± 8.160 | 0.7783 | |
| Length of Front Flipper, cm Figure 3 | Exponential | 43 | 21.47± 1.467 | -0.07445 ± 0.02306 | 50.57 ± 10.07 | 0.6887 | 47.2 ± 1.9<br>(n = 8)<br>Max. = 55 |
| | Logistic | | 21.73 ± 1.355 | -0.1576 ± 0.04247 | 45.12 ± 4.622 | 0.6901 | |
| | Gompertz | | 21.60 ± 2.598 | -0.1157 ± 0.04094 | 47.03 ± 6.263 | 0.6896 | |
| | Linear | | 23.44 ± 1.100 | m = 1.3144 ± 0.1368 | | r = 0.8322 | |
| Length of Rear Flipper, cm | Linear | 43 | 15.17 ± 0.8823 | m = 1.030 ± 0.1096 | | r = 0.8262 | 28.7 ± 0.9<br>(n = 7), Max. = 32 |
| **Baculum** | | | | | | | |
| Baculum Length, mm Figure 4 | Exponential | 35 | -12.5 ± 17.05 | -0.2695 ± 0.05170 | 122 ± 3.944 | 0.7871 | 112 ± 6.4<br>(n = 14)<br>Max. = 134.7 |
| | Logistic | | 21.8 ± 4.660 | -0.4653 ± 0.06346 | 119 ± 2.959 | 0.8105 | |
| | Gompertz | | 14.5 ± 5.53 | -0.3601 ± 0.05341 | 120 ± 3.319 | 0.8012 | |

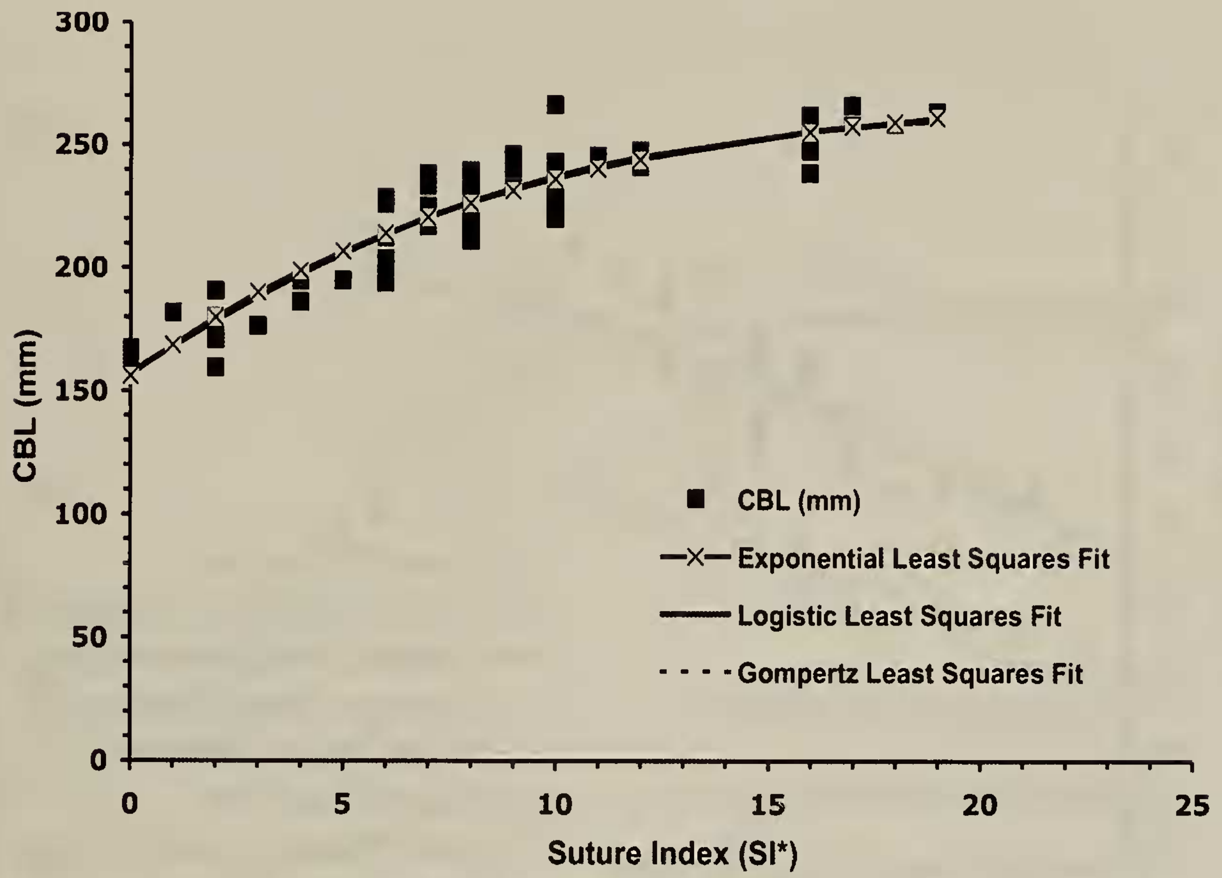

**Figure 1. Non-Linear least squares fits to plots of Condylobasal Length (CBL) (mm) vs. Suture Index (SI*) (n = 63). All the fits were good (Coefficients of determination R2 > 0.8) and the model parameters are tabulated in Table 3.**

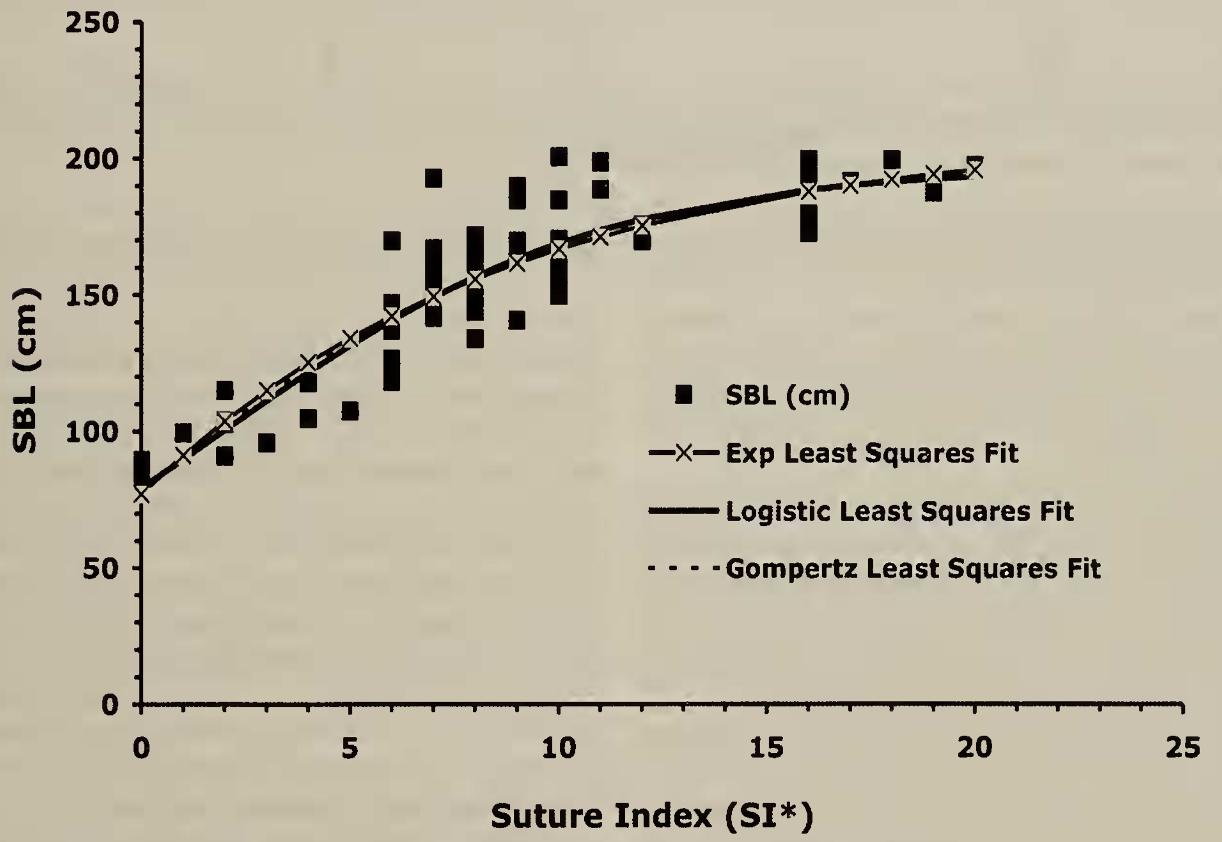

**Figure 2. Non-Linear least squares fits to plots of Standard Body Length (SBL) (cm) vs. Suture Index (SI*) (n = 63). As for Fig. 1 all the fits were good (R2 = 0.76) and the model parameters are tabulated in Table 3.**

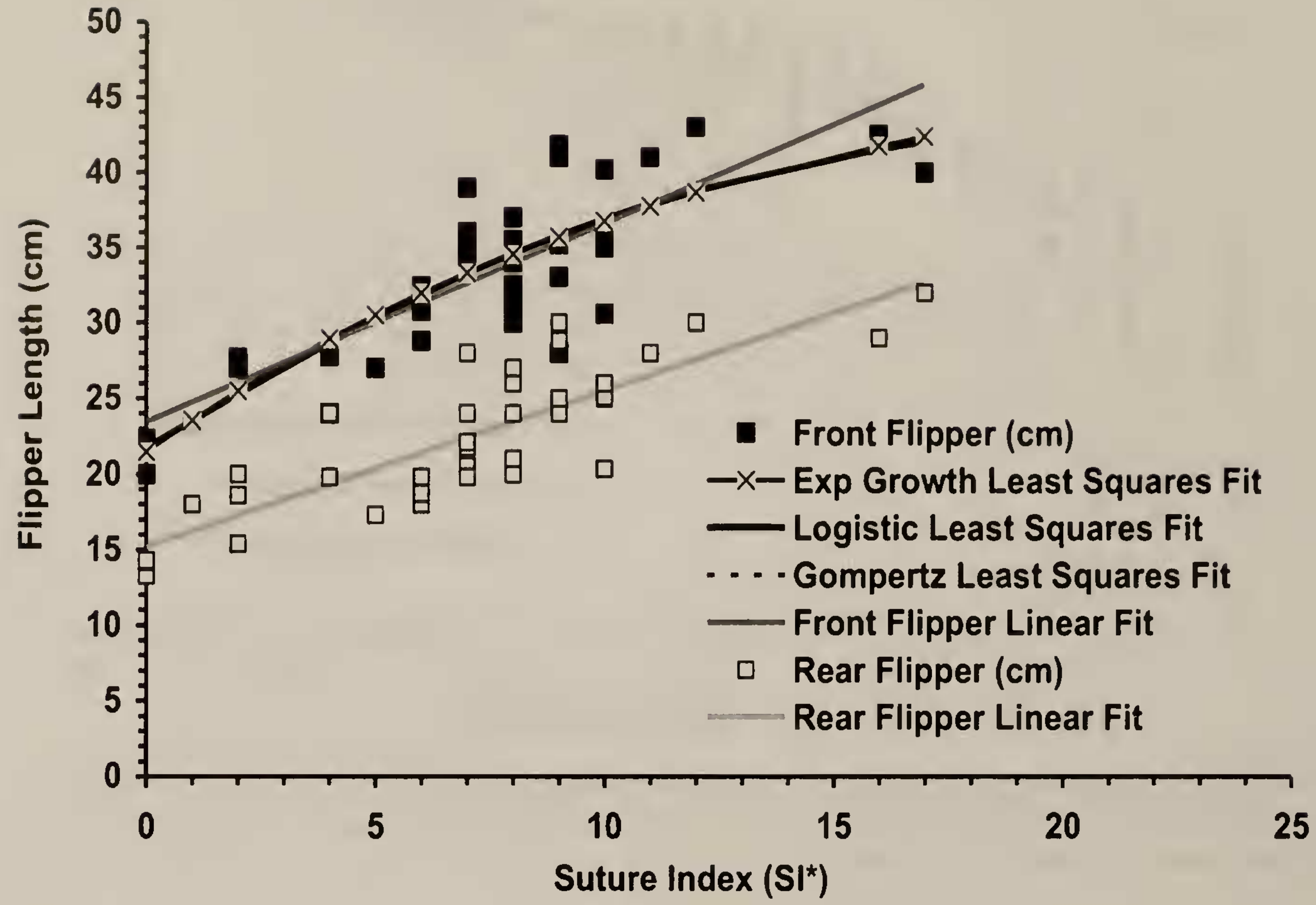

**Figure 3. Front and Rear Flipper lengths vs. Suture index (SI*). Non-linear fits (Exponential, Logistic and Gompertz models) of Front Flipper length (cm) vs. SI* and also a linear fit to the same data (n = 42) are shown. A linear fit is shown for Rear Flipper length vs. SI*.**

Plots of the three models in Figs. 1 & 2 are virtually identical and almost completely overlap each other. The initial sizes (the 'pupsize') and the asymptotic maximum sizes determined using the three models were consistently not significantly different to one another, regardless of which fitting curve model was used (Table 3).

Plots of Front Flipper Length vs. **SI*** and Rear Flipper Length vs. **SI*** (Fig. 3) are more problematic. Satisfactory fits to the Exponential, Logistic and Gompertz models could be achieved for the Front Flipper vs. **SI*** data, however Fig. 3 clearly shows that fitted lines are very close to linear with very little curvature. The relative errors of the fitted parameters are large even though $R^2 > 0.67$ (Table 3) suggesting that the three parameter models are overly complex for the data available. A simple linear relationship of Flipper Length vs. **SI*** also fits the data very well ($m = 1.3144 \pm 0.1368$, $R^2 = 0.6926$) and is a fundamentally simpler model using only two parameters. The plot of Rear Flipper length vs. **SI*** does not fit the Exponential, Logistic and Gompertz models very well because estimates of the initial size and the asymptotic final size are not very precise and the fitted lines are almost linear. Fitting the simple linear relationship is more realistic (Fig. 3): based on the principle of adopting the simplest model consistent with the data. The linear fit has a correlation coefficient ( r) value of 0.8262 and a slope of 1.030 ± 0.1096 ($p << 0.0005$).

Some conclusions can be drawn about the relative growth rates of front vs. rear flippers. Front Flipper and Rear Flipper measurements on the same individual are highly correlated ($r = 0.8288$, $n = 43$) with a slope of 1.05 ± 0.111, indicating that both flippers increase in length by the same amount although from different initial lengths as the animal grows larger.

The exponential kinetic parameter (k) calculated for the Exponential, Logistic and Gompertz models are different to one another but the models show some consistent patterns (Table 3). The k-values for

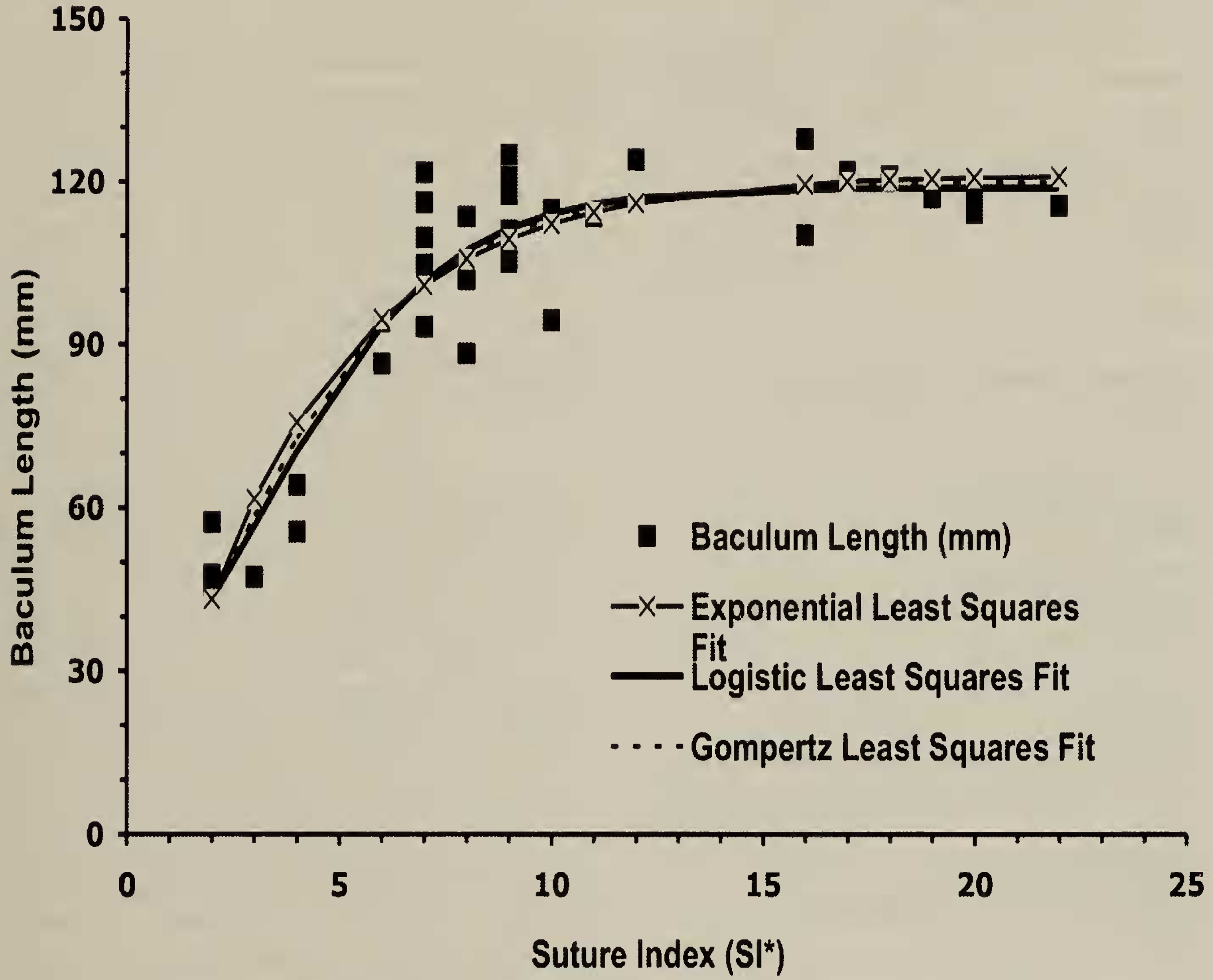

**Figure 4. Non-Linear least squares fits to plots of Baculum Length (mm) vs. Suture Index (SI*) (n = 35). As for Figs 1 and 2 all the fits were good (R2 > 0.77). The model parameters are tabulated in Table 3.**

the exponential model for length parameters such as **CBL**, Ramus length and **SBL** are all very similar (k ≈ -0.1). Similarly, the Logistic and Gompertz k-values are for **CBL**, Ramus and **SBL** are similar to one another (k ≈ -0.18 for logistic model and k ≈ -0.15 for the Gompertz model). The exponent k-parameters for the three models related to the width of the animal, in the skull (Bizygomatic breadth and Mastoid breadth) and the Front flipper are also similar indicating that increases in the size of these parameters follow similar kinetics.

Growth of the baculum (Fig. 4 and Tables 3 and 4) has conspicuously different kinetics to the skull and body size parameters. Plots of the Exponential, Logistic and Gompertz models are virtually identical and almost completely overlap each other. The three models predict very similar asymptotic maximum sizes (about 120 mm). Estimates of the initial size are plausible for the Logistic and Gompertz models (15 & 22 mm respectively). The Exponential model gives a spurious negative initial value that is not significantly different to zero. All three models show that the asymptotic baculum size is reached very quickly when animals attain an **SI*** of about 7 or at about 5 and a half years old based on the relationship between age and **SI*** (Stewardson et al. 2011b). Thus, the baculum length very rapidly reaches an asymptote much earlier than the skull parameters and the other body measurements.

Biologists generally have a better grasp of growth kinetics expressed as half-times ($t_{0.5}$) rather than exponential constants. Table 4 shows the half-times calculated from the exponential growth model shown in Table 3 for incremental growth of the skull and

**Table 4: Incremental Growth and Estimated Time to Reach One Half of Full Incremental Growth of Male South African Fur Seals. Half-times in years were calculated from the relationship of SI* to Age (y) found by Stewardson et al. (2011).**

| Parameter | Fitting Model | Number of Animals (n) | Incremental Growth Asymptote | Exponential Constant (k) | Half-Time on SI Basis (SI*) | Half-Time (y) |
|---|---|---|---|---|---|---|
| **Skull** | | | | | | |
| Condylobasal Length (**CBL**), mm<br>Figure 1 | Exponential | 64 | 120 ± 9.57 | -0.1115 ± 0.007527 | 6.22 ± 0.420 | 5.02 ± 0.421 |
| Ramus Length, mm | Exponential | 60 | 103 ± 9.51 | -0.09730 ± 0.008689 | 7.12 ± 0.636 | 5.76 ± 0.549 |
| Bizygomatic Breadth (**Zyg**), mm | Exponential | 61 | 96.4 ± 15.9 | -0.06495 ± 0.009577 | 10.7 ± 1.57 | 8.63 ± 1.305 |
| Mastoid Breadth, mm | Exponential | 59 | 93.0 ± 11.4 | -0.07436 ± 0.008803 | 9.32 ± 1.10 | 7.54 ± 0.927 |
| **Body** | | | | | | |
| Standard Body Length (**SBL**), cm<br>Figure 2 | Exponential | 64 | 134 ± 13.6 | -0.1114 ± 0.01387 | 6.22 ± 0.775 | 5.03 ± 0.648 |
| Length of Front Flipper, cm<br>Figure 3 | Exponential | 43 | 29.1± 10.2 | -0.07445 ± 0.02306 | 9.31 ± 2.88 | 7.53 ± 2.35 |
| Length of Rear Flipper, cm | Exponential Model Inappropriate | | | | | |
| **Baculum** | | | | | | |
| Baculum Length, mm<br>Figure 4 | Exponential | 35 | 134 ± 17.5 | -0.2695 ± 0.05170 | 2.57 ± 0.493 | 2.08 ± 0.405 |

body parameters and for the baculum length. The half time in terms of **SI*** was converted to chronological age using the regression relationship found previously (Stewardson et al. 2011). Parameters related to the 'length' of the animal (**CBL**, Ramus length and **SBL**) all have half times for incremental growth of about 5 years. 'Width' parameters more related to cross-section of the animals (Bizygomatic breadth, mastoid breadth and front flipper length) all have half times of about 8 years. This is consistent with the seals reaching adult body length rather quickly but increase considerably in mass as they mature. Growth of the baculum to adult size is very rapid with a half-time of only about 2 years leading to the completion of growth of the baculum in males at an age of ≈ 5.5 years.

## DISCUSSION

As with other polygynous breeding pinnipeds, which exhibit, pronounced size dimorphism, full reproductive status (social maturity) is deferred until full size and competitive vigour are developed (Bartholomew 1970; McLaren 1993) although the baculum rapidly reaches adult size (Fig. 4). Male South African fur seals attain social maturity at 8-10 y (Stewardson et al. 1998, 2008). Although some males may grow to **SBL** = 220 cm or more (Rand 1949), asymptotic **SBL** size is estimated to be between 198 and 220 cm (present study) which agrees well with estimates based on **SBL** vs. known age (Stewardson et al. 2009).

Information on asymptotic size (Table 3) of parameters such as **CBL** and **SBL** are advantageous for comparisons among different species of pinnipeds because average size (including average adult size) may be more influenced by sampling biases, e.g., larger or smaller individuals may be over-represented in certain year/suture classes (McLaren 1993). Estimates of asymptotic size from plots of size vs. **SI*** appear to be of practical value in life history studies of the South African fur seal and may prove to be of value for studies of the Australian fur seal

(*Arctocephalus pusillus doriferus*). Asymptotic size estimates derived from plots of size vs. **SI*** in the present study and asymptotic sizes based upon plots of size vs. chronological age were found to be consistently very similar (Stewardson et al. 2008, 2009). In the case of growth of the baculum vs. age of animals it was not possible to calculate the asymptotic size of the baculum from plots of baculum size vs. age because of a lack of baculum measurements for animals with a definitive age greater than 10 years or for subadult males (2 to 6 y) (Stewardson et al. 2010a). Data for baculum size vs. suture index (**SI***) has allowed us to show that baculum size reaches an asymptote in animals at about 6 y. Baculum size might be of some value in classifying males into juvenile, subadult and adult classes but is of limited value for age determination.

The major advantage of using suture index (**SI***) information as a substitute for chronological age in growth studies is the limited number of animals that have been aged based on tagging or upon dentition (Stewardson et al. 2011a). More information on animals older than 12 y is needed. Tagging is the definitive source of age information. Dentine-GLG methods of aging South African fur seals not only has inherent limitations because of pulp cavity closure (Stewardson et al. 2011a) but also has a significant failure rate. Seventeen out of 48 specimens used in our studies of South African fur seals could not be aged at all because dentine growth lines could not be recognised in prepared sections of canines. Oosthuizen (1997) found that the cementum of canines was too thin for reliable aging. Suture information is relatively easy to obtain on skulls and is non-destructive.

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